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Contents

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STUDIES ON CESTODES OF THE GENUS *TRIAENOPHORUS* FROM FISH OF LESSER SLAVE LAKE, ALBERTA

IV. THE LIFE OF *TRIAENOPHORUS CRASSUS* FOREL IN THE SECOND INTERMEDIATE HOST[1]

BY RICHARD B. MILLER[2]

Abstract

The plerocercoids of *Triaenophorus crassus* encyst normally in the flesh of fishes of the genus *Leucichthys;* the whitefishes, *Coregonus clupeaformis* and *Prosopium oregonium,* are common alternative hosts in Lesser Slave Lake. Elsewhere lake trout, *Cristivomer namaycush,* and possibly the inconnu, *Stenodus leucichthys,* may occasionally serve as hosts.

The procercoids arrive in the stomach of their second intermediate host while in the body cavity of *Cyclops bicuspidatus.* When they are liberated by digestion, the majority apparently enter pyloric caeca, penetrate these, cross the body cavity, and enter the flesh, where encystment as the plerocercoid takes place. The evidence for these movements is only partial. The plerocercoids encyst in the flesh in July each year. They remain three or four years and then disappear by drying up or being reduced to small calcareous nodules.

The number of plerocercoids per fish increases with the age of the fish up to five or six years.

In Part I of these studies (3) the adult of *Triaenophorus crassus* Forel was described; an account of its life in the definitive host, *Esox lucius* L., and the maturation and release of the eggs in late April and early May was given. In Part II (4) the coracidia and the procercoid stage in *Cyclops bicuspidatus* Claus were described. This paper gives an account of the plerocercoid stage in the coregonine fish, *Leucichthys* sp., and the completion of the life cycle of the parasite.

The Second Intermediate Hosts

The encysted plerocercoids of *T. crassus* in the flesh of coregonine fishes are the most familiar stage in the life history. Cooper (1) found them in the muscles of *Leucichthys artedi* (Le Sueur); Hjortland (2) reported them from *Leucichthys tullibee* (Richardson); Newton (7) in an extensive survey of Manitoba fishes reported these cysts from *Leucichthys tullibee, L. zenithicus* (Jordan and Evermann), *L. nipigon* Koelz, *L. nigripinnis* (Gill), and *Coregonus clupeaformis* (Mitchill). In the present investigation the cysts were studied mainly in *Leucichthys* sp. (probably *tullibee*) but the parasites were also found in the flesh of *Coregonus clupeaformis* and *Prosopium oregonium* Jordan and

[1] *Manuscript received April 13, 1945.*
Contribution from the Department of Zoology, University of Alberta, Edmonton, Alta.
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Snyder; occasionally a cyst was found in the visceral peritoneum of the stomach of young pike (*Esox lucius* L.). In a collection of parasites from Great Slave Lake, sent to the author by Dr. D. S. Rawson, cysts of *T. crassus* from the flesh of the lake trout, *Cristivomer namaycush* (Walbaum), were found; a plerocercoid from the inconnu, *Stenodus leucichthys* (Güldenstadt), in the same collection, while lacking the scolex, is almost certainly *T. crassus*. Scheuring (10) records plerocercoids of *T. crassus* from three European Salmonidae.

It is apparent that in this country all species of *Leucichthys* and four, possibly five, other fishes are capable of acting as second intermediate hosts for *T. crassus*. The author believes, however, that the species of *Leucichthys* are the original hosts; the others are incidental or adventitious hosts. There is considerable evidence in support of this view. *Leucichthys* spp. are plankton feeders throughout life and thus the first intermediate host, *Cyclops bicuspidatus*, is part of their normal food. This is true of none of the other possible hosts. In any lake where parasitized *Leucichthys* and *Coregonus* occur the former are always more heavily parasitized; this fact shows that *Leucichthys* is more readily infected. Finally, in Alberta, lakes Wabamun, Ste. Anne, Newell, Chin, McGregor, Pigeon, Muriel, and Buck all contain whitefish, pike, and *Cyclops bicuspidatus* but no *T. crassus*; the missing factor is *Leucichthys*. It seems reasonable to conclude that without *Leucichthys* spp. the life cycle could not be carried on; pike seldom eat whitefish but do consume large numbers of tullibee in western lakes. Scheuring (9) formed a similar conclusion with regard to the perch in Europe; of 30 sometime second intermediate hosts for *T. nodulosus* (Pallas) he decided that all but the perch were incidental hosts.

Morphology of the Cyst and Plerocercoid

The plerocercoids of *T. crassus* have frequently been found in European fishes not enclosed in cysts but naked in the flesh like *Diphyllobothrium latum* (Linnaeus). The author has found such unencysted plerocercoids in young *Leucichthys* sp. from Lake Winnipeg. In this country, however, the cyst is almost universally present. They have been fully described by Cooper (1), Hjortland (2), and Newton (7) in North America, and are now so well known as to need little further description in this paper. Each consists of a wall of connective tissue supplied by the host; inside, surrounding the coiled plerocercoid, is a thick albuminous fluid made up of digesting host tissue and excretory products from the worm. The cysts are extremely variable. Figs. 1 to 9 are a summary of the various sizes and shapes encountered while measuring some 200 cysts. The symmetrical straight cysts (Fig. 1) occurred in 20% of the lot; the asymmetrical straight cysts (Fig. 2), 25%; the dumb-bell-shaped (Fig. 3), 5%; curved, hooked, and forked cysts (Figs. 4, 5, and 6) together amounted to 35% of the total; the remaining types, perforate, degenerate, and twins (Figs. 7, 8, and 9) occur rarely and together made up only 15% of the total. Contrary to Newton's views (7) the author observed

no correlation between shape of cysts and degree of crowding; forked and perforate cysts did occur in fish where only two or three other cysts were present.

FIGS. 1 to 9. *Drawings of all the types of cysts of T. crassus encountered during the investigation. Explanation in text.*

The cysts occur in the myomeres; usually one cyst is wholly within a myomere but occasionally a cyst extends across two. Newton (7) gives a diagram showing cyst distribution in the flesh of a whitefish (Fig. 5 of his paper). He found 80% in the epaxial muscles between the head and the dorsal fin, 10% in the remaining epaxial muscles and 10% in the hypaxial muscles. The findings in the present investigation are in agreement with this except that cysts almost never occur behind the anus, but only in those parts of the flesh bordering on the coelom. In fact they are distributed mainly in the flesh nearest their origin, the stomach of the fish. An interesting confirmation of this is found in the consistently greater number of cysts on the right side as shown by the following figures. In 645 tullibee from Lesser Slave Lake 2858 cysts occurred on the right side and 2149 on the left. The first part of the intestine of coregonine fishes lies along the left side of the

stomach separating it from the left body wall; the right side of the stomach lies directly against the right body wall; more than half the cysts form in the flesh on the right side.

Each cyst normally contains a single plerocercoid; in about 4000 cysts examined in this study only three have been found (Fig. 9) that contained two plerocercoids.

The plerocercoid is a long (up to 300 mm.), thin (1 mm.), unsegmented worm that has a fully developed scolex similar to that of the adult. Young plerocercoids still possess a frontal gland, which opens at the tip of the scolex. Sex organs are never developed. Often a cauda is present; this is a posterior appendage of variable length, characterized by poorly developed muscles and parenchyma and presenting a degenerate appearance. The great variability of the plerocercoid and its cauda appears to be related to age; this relationship is discussed in the next section.

Changes in the Plerocercoid with Age

Early in this study the great variation in the size of the cysts and the length of the enclosed plerocercoid was observed. Large, thin-walled cysts had the longest plerocercoids and pale, non-granular contents; smaller, thicker-walled cysts contained shorter plerocercoids, often provided with a cauda, and yellowish (rarely black) cyst contents with hard calcareous particles. Still other cysts, smaller yet, contained no worm and had become completely calcareous. In an effort to interpret these observations all the cysts were dissected out of 50 tullibee; the length, maximum diameter, and volume of each was measured; the length and condition of each plerocercoid was recorded and the nature of the fluid content of the cysts was noted. The age of the tullibee from which each cyst was taken was determined by scale reading. In this way 243 cysts and plerocercoids were measured. The data collected show that a strong correlation exists between cyst volume on the one hand and the condition of the plerocercoid and the nature of the fluid content of the cyst on the other. Large cysts (0.07 to 0.12 cc. volume) contained large (70 to 130 mm.) plerocercoids, with short (0 to 30 mm.) caudae; their fluid contents were pale and non-granular. Smaller cysts (0.03 to 0.06 cc. volume) contained smaller plerocercoids (36 to 68 mm.) with long caudae (more than one-half the length of the worm); the fluid contents were yellow and contained large calcareous particles. The smallest cysts (less than 0.03 cc. in volume) sometimes contained no plerocercoid, sometimes just the scolex or scolex hooks, and the content had become almost solid and orange in colour.

The author's interpretation of these findings is that the large cysts contain young plerocercoids, recently arrived in the flesh; the small cysts are those of older plerocercoids, starting to degenerate; the smallest are very old and represent the final step in the complete degeneration of the plerocercoid.

The age of the cyst bears some relation to the age of the host; in four-year-old tullibee one-third of the cysts showed signs of degeneration; in older fish

(five to eight years) approximately 50% of the cysts showed signs of degeneration. The bearing of these facts on the length of life of the plerocercoid will be discussed later.

The observations recorded above throw some light on the nature of the cauda. The literature contains statements of the size of this structure that are apparently contradictory. Cooper (1) and Hjortland (2) both remarked on the variability of the cauda. The latter put forward the suggestion that young plerocercoids had long caudae, which were used up during subsequent growth. The present writer takes quite an opposite view; the evidence, given above, indicates that the cauda grows longer with age and represents the progressive degeneration of the plerocercoid from the caudal end toward the scolex. Figs. 10, 11, and 12 show three stages in this process; Fig. 10

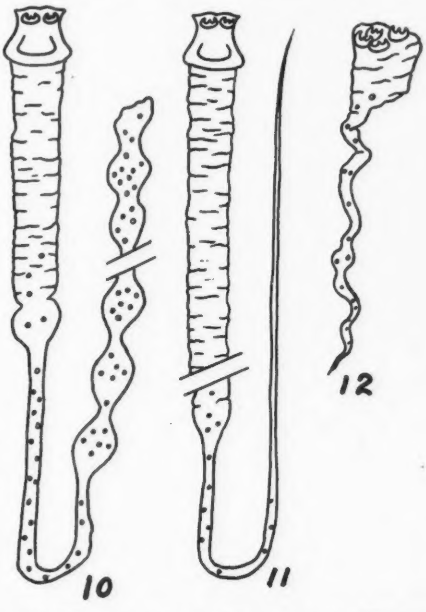

FIG. 10. *A plerocercoid of T. crassus removed from the cyst. The irregular cauda, making up more than half of the worm, is shown.*

FIG. 11. *A plerocercoid of T. crassus in which the cauda has become reduced to a fine filament.*

FIG. 12. *A plerocercoid of T. crassus in which degeneration has proceeded the full length of the strobila and has involved the scolex. This plerocercoid was dead.*

shows a young cauda, characterized by bloating and irregular swellings; Fig. 11 is a later stage where the cauda has become a long filament; in Fig. 12 the degeneration has proceeded to the scolex.

The author's speculations on the nature of the cauda in Part I of these studies (3) were substantially correct in conclusion, i.e., that the cauda is the product of the progressive degeneration of the plerocercoid beginning at the

posterior end. His belief that the cauda was produced during the first year of the plerocercoid's life must be revised in the light of evidence, given below, that the plerocercoid lives for at least three years. The cauda is probably still quite small at the end of the first year.

Relation Between Number of Plerocercoids and Age of Host

Mr. H. J. Hoffman, of the Minnesota Department of Agriculture, Dairy and Food, was called upon by his state to set up an inspection system for *Triaenophorus* cysts in the tullibee of Lake of the Woods. His inspectors kept records of the weights of all fish they examined; Mr. Hoffman discovered from these records that there was a definite correlation of numbers of cysts with weight of host. The heavier the fish, the greater the number of cysts it contained. Mr. Hoffman very kindly sent the author copies of his inspectors' reports from Lake of the Woods. A perusal of these reports led the author to begin similar observations on the tullibee of Lesser Slave Lake; in this work, however, the age of the fish was used rather than the weight. The findings to date are shown in Table I.

TABLE I

THE NUMBER OF CYSTS OF *T. crassus* PER 100 TULLIBEE OF EACH YEAR CLASS IN LESSER SLAVE LAKE

Date of capture	Year classes									
	1943	1942	1941	1940	1939	1938	1937	1936	1935	No. of fish examined
Jan. and Feb., 1944	—	—	—	82	760	1078	910	1012	437	332
May 1 to June 15, 1944	0	18	—	20	600	1055	608	940	633	113
July 25, 1944	—	—	—	475	970	1447	823	1567	—	50
Oct., 1944	0	0	200	370	1460	1175	1129	1333	—	50
Jan. and Feb., 1945	—	5.6	28.5	733	770	880	835	540	100	100

From Table I it can be seen that no parasites were found in yearling tullibee, small numbers in two-year-olds and increasing numbers each additional year of life up to five or six years. In general, fish that had experienced six springs (six exposures to *Triaenophorus*) were the most heavily parasitized (the year class of 1938 collected January, February, May, and June, 1944, and the year class of 1939 collected October, 1944). Further exposures apparently do not materially increase the number of parasites; fish older than five years were not much more heavily parasitized and the eight-year-olds appear to have significantly fewer parasites. The bearing of these observations on the length of life of the plerocercoid is discussed in a special section below.

The correlation of cyst numbers with age is not so clear-cut in whitefish, a situation that one might expect in an incidental host. Table II shows the distribution of cysts according to age of host for 490 whitefish collected by Alberta Fisheries officials from Lesser Slave Lake in September, 1944.

Although somewhat erratic, the figures in Table II do show a definite increase in number of cysts with increasing age in whitefish.

TABLE II

THE NUMBER OF CYSTS OF *T. crassus* PER 100 WHITEFISH OF DIFFERENT AGES

Age of fish	No. of fish examined	Cysts per 100 fish
2	1	0
3	52	240
4	203	65.5
5	106	94.3
6	40	260
7	34	882
8	39	1556
9–11	15	453

Length of Life of Plerocercoids

The question of the length of life of the plerocercoids of *T. crassus* is an important one because of its bearing on the control problem. Probably the most practical control measure for this tapeworm is the elimination of the pike (5); if such elimination were accomplished it would be important to know how long the cysts present in the tullibee and whitefish in the control area would remain alive to spoil the fish for market purposes or to re-infect a possible new population of pike. In the preceding sections of this paper two facts that have a bearing on this question are brought out. These are first, the accumulation of cysts up to a certain age in tullibee and, second, the criteria by which one may recognize a plerocercoid that is starting to degenerate and a plerocercoid that is well along the path of ultimate disappearance.

The data for the accumulation of cysts in tullibee with age are shown in Table I. They show that the number of cysts per fish increases very slightly or not at all beyond six summers of exposure to infestation. Since the number of cysts per fish does not increase beyond this age but, in many, tends to decrease, it is obvious that the cysts are disappearing as fast as, or faster than, they are forming anew; for, if this were not so, the number of cysts would continue to increase with each year of life because the feeding habits of tullibee are not known to change during their adult lives.

The argument in the preceding paragraph establishes the fact that the cysts do disappear from the flesh. The observations on the change in the cyst and plerocercoid with age, described in a previous section, tell *how* the disappearance takes place—by the gradual absorption of the cyst by the host leaving in the end a small calcareous nodule and possibly, in some instances, nothing at all. To learn *when* the cyst disappears is the next problem. Tullibee during their first summer are never found in the shallow, shoreward waters of Lesser Slave Lake but in small, surface-swimming schools. It has been shown (4) that *Cyclops bicuspidatus* infected with procercoids of *T. crassus* are in the

shallow water, near shore. Therefore it is very unlikely that tullibee become infested during their first summer. The data in Table I show that no yearlings were found that were infested; it can be concluded, then, that very few tullibee become infested during their second summer (as yearlings). This is perhaps due to the relatively small numbers of copepods such small fish would consume. Substantial numbers of cysts appear for the first time in fish that have had three summers' exposure to the parasites. The maximum occurs in fish that have had six summers' exposure. The inference is obvious—the plerocercoids live at least three years. The failure of the numbers of cysts to increase beyond the sixth summer suggests that the plerocercoids begin disappearing when they are four years old.

In 243 cysts dissected from tullibee of known age the least number of cysts showing signs of degeneration (about one-third the total) was found in the fish that had five summers' exposure. In the older fish approximately half the cysts showed such signs.

In the tullibee collected October, 1944, no old cysts were found in fish younger than five years old. The first obviously degenerate cysts were found in the five-year-olds, i.e., fish that had had six summers' exposure to infestation. These facts point to the same conclusion reached in the argument above, namely, that the cysts begin to disappear in their fourth year of life and therefore live at least three years.

Time of Cyst Formation

The data used above to establish the life span of the plerocercoids also provide the answer to the question of what time of year the cysts form in the flesh. Referring again, therefore, to Table I, the infestation of the year class of 1940 is specially instructive. In January and February of 1944, fish of this year class were found to contain 82 cysts per 100 fish; in May and June, 20 were found, a number of no probable significant difference. In July, however, only one month later, a tremendous jump to 475 cysts per 100 fish took place. Figures of the same order of magnitude were observed in October and in January and February of 1945. Obviously a new crop of cysts was acquired sometime during late June or July.

In a previous paper (4) it has been shown that the first *Cyclops bicuspidatus* infected with procercoids of *T. crassus* are present in the lake about May 15; peak numbers of infected copepods occur about the end of May. The parasite therefore requires approximately two months to get from the procercoid stage in *Cyclops bicuspidatus* to the encysted plerocercoid stage in the tullibee. In the next section a fragmentary account of this transformation is given.

The Change from Procercoid to Plerocercoid

That the procercoids of *T. crassus* first reach the tullibee by being swallowed while inside their *Cyclops* hosts is beyond doubt; their liberation by the digestion of the *Cyclops* is the next step. The history of the procercoid from

then on is a matter for conjecture. It has been shown above that approximately two months after they are swallowed the parasites appear as encysted plerocercoids in the flesh. A number of observations indicate that the procercoids begin by penetrating the wall of a pyloric caecum of the stomach. Several plerocercoids have been found encysted in the visceral peritoneum of the pyloric region of the stomach and several in the parietal peritoneum adjacent to the stomach; such encysted worms have been found at no other places in the body cavity. On four occasions small larval cestodes have been found free in the adipose tissue around the pyloric caeca of tullibee stomachs. One of these worms had developed scolex hooks and was unquestionably *T. crassus*. Another indication is that more cysts occur on the right side of the body than on the left; the stomach of coregonine fishes lies against the right side of the coelom.

Rosen (8) observed stomach wall penetration by procercoids of *Triaenophorus nodulosus* (Pallas) in young perch; the author (6) has seen evidence of the same thing for *T. nodulosus* in young burbot. The procercoid of *T. crassus*, like that of *T. nodulosus*, is provided with a conspicuous frontal gland, which probably secretes (as it does in *T. nodulosus*) a ferment for use in digesting tissue of the gut wall. From these facts and observations it seems safe to conclude that the procercoids of *T. crassus* do penetrate the stomach wall in their journey to the flesh. Nevertheless, direct observation was desirable and an experiment was designed to provide it. In this experiment yearling coregonines (tullibee and whitefish) held in an outdoor tank were each fed two *Cyclops bicuspidatus* containing procercoids of *T. crassus*. The copepods were administered with a medicine dropper. The experiment was a failure as it developed that the fish were so nervous in captivity that their digestive systems stopped functioning. In all but one the copepods were undigested. In the one exception, a whitefish that was killed the day following the force feeding, a single procercoid was recovered free in the lumen of the stomach.

Some information has been obtained from an examination of stomachs of tullibee collected by netting during May and June. As mentioned above four larval cestodes were found in adipose tissue scraped from the pyloric caeca of tullibee stomachs. The first was found on May 21; it resembled the procercoid from *Cyclops bicuspidatus* exactly except that it had no cercomere and was somewhat larger—792μ in length. A similar worm, 1.2 mm. long, was found on May 30 and a third, 704μ long on June 1. On June 7, a worm 3 mm. long was found protruding from the tip of a pyloric caecum; one end was firmly embedded in the muscle layer of the caecum. It had a fully developed scolex with four typical *T. crassus* hooks. It seems probable that this was an unusual occurrence in which the parasite failed to get entirely through the caecum wall. These observations indicate that the procercoids enter the pyloric caeca and make their way through them into the coelom.

A number of tullibee stomachs collected in May and June were embedded in celloidin and sectioned serially. Sections of larval cestodes showed up among

the pyloric caeca of two stomachs; these are probably *T. crassus.* In one stomach, collected May 31, a small canal through the wall of one pyloric caecum was found. A section through this canal is shown in Fig. 13. The canal has a fibrous wall resembling the lining of the pits in the pike gut made by adults of *T. crassus:* it is probably the passage made by a procercoid through the pyloric caecum.

A completed cyst never contains an incomplete plerocercoid. The transformation from procercoid to plerocercoid occurs before encystment. Evidence given above shows that after traversing the stomach wall the parasite is still little larger than the procercoid. The part of the fish's body in which the growth to the plerocercoid takes place is unknown. The flesh of many tullibee has been carefully examined but no non-encysted specimens of *T. crassus* have been found. The growth to the plerocercoid stage must take place in the body cavity; the worms must enter the flesh just before encystment. Larval cestodes lacking a developed scolex but beyond the procercoid stage were found in the adipose tissue of the pyloric caeca in some of the serially sectioned stomachs. Possibly these are developing plerocercoids of *T. crassus.*

The Change from Plerocercoid to Adult

The completion of the life cycle of *Triaenophorus crassus* is achieved when a pike swallows a tullibee (or other host) containing the encysted plerocercoids. The pike digests the cyst wall and the plerocercoid is liberated. The process has been witnessed by feeding to captive pike pieces of tullibee flesh containing plerocercoids. Thirty-nine pike were so treated; the flesh was pushed into their stomachs with a glass rod. The experiment was done during late May and early June, a period when the pike were known to be almost free of *T. crassus* (3). Fifteen of the pike failed to digest their enforced meals; evidently in captivity they were afflicted with the same nervous indigestion encountered in the coregonines that refused to digest copepods. However, pike are more robust, and successful recoveries of established worms were made in eight individuals.

After liberation from the cyst the plerocercoid at once begins to bury its scolex in the gut lining choosing always the region just distal to the pylorus. Three days after feeding the plerocercoids were already fairly strongly attached, though not to the same extent as mature worms. All were very much smaller than plerocercoids in the cyst. Apparently the posterior one-half to two-thirds of their strobilae are lost almost immediately. So rapid is the loss that it seems likely that the missing portion is shed and not absorbed. The tattered appearance of the caudal end of each plerocercoid lends weight to this view.

The subsequent growth to sexual maturity, spawning, and death the next spring have been described in Part I of these studies (3).

PLATE I

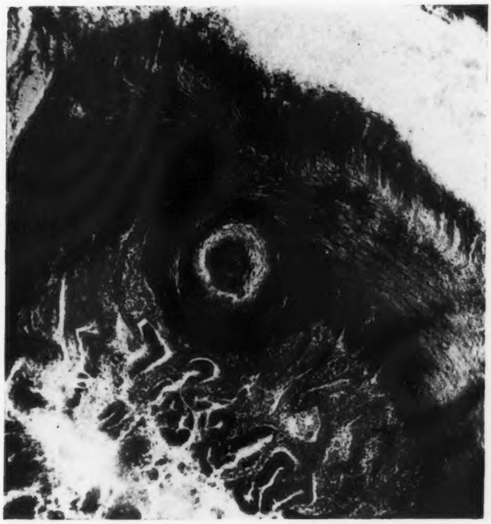

FIG. 13. *Photomicrograph of part of a section through the pyloric region of the stomach of a tullibee. The canal in the muscle of one of the caeca is believed to have been made by a procercoid of T. crassus in its passage through the wall of the caecum .* (× 53)

Further Notes on the Adult

In his monograph on the Pseudophyllidea, Cooper (1) reports *T. robustus* (synonym of *T. crassus*) from the intestine of the burbot, *Lota lota maculosa* (Le Sueur), as well as the usual adult host, the pike. The burbot has, therefore, been accepted as an alternative host for this cestode. The present writer does not question Cooper's record but does believe that the burbot is not an alternative host for *T. crassus*. Cooper's record was of an immature specimen without sex organs—a plerocercoid. It seems very probable that this worm had been recently swallowed and if left for a time would have been digested or evacuated. In Lesser Slave Lake burbot feed almost exclusively on tullibee, which average about nine cysts of *T. crassus* per fish. Yet, although over 100 burbot have been carefully examined in summer and winter, not a single *established* plerocercoid has been found. Occasionally digested cysts and liberated, but moribund, plerocercoids were encountered and such was, perhaps, the nature of Cooper's record.

The author feels it is safe to conclude that the pike, *Esox lucius* L., is the only host for the adult of *Triaenophorus crassus* in lakes of Western Canada.

Acknowledgments

In addition to the financial aid received from the Government of the Province of Alberta the author would like to express his thanks to Mr. H. J. Hoffman of the Minnesota Department of Agriculture, Dairy and Food, who sent copies of his inspectors' records for tullibee in Lake of the Woods.

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Abstract:—**An abstract of not more than about 200 words, indicating the scope of the work and the principal findings, is required.**

Illustrations

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